# *NOTHOFAGUS CUNNINGHAMII* ECOTONAL STAGES

## Buried Viable Seed in North West Tasmania

By TRUDA M. HOWARD*

ABSTRACT: The buried viable seed from three vegetation types at West Downs, Surrey Hills, North West Tasmania, was germinated and species types and numbers recorded. The three vegetation types were a *Poa gunnii* dominated grassland, a closed *Nothofagus cunninghamii* forest and an *Acacia melanoxylon* dominated ecotone between these two, on a kraznozem derived from basalt at 1900 ft (579 m).

Of the seeds germinating from the soil, the numbers diminished with depth, woody species were poorly represented, and in the two forest soils, grasses, rushes, sedges and herbs not present in the vegetation were abundant.

Difference between the species composition of the stored seed and the present vegetation were found to correlate with seral stages observed after burning or logging of forests in the Surrey Hills district.

## INTRODUCTION

Observations made on the viable seed stored in a suceessional series of old field and forest soils by Oosting and Humphreys (1940) led them to the eonclusions that viable seeds in the soil undergo suceession as do the plants above ground. They also found that viable buried seed can to some extent indieate the probable species present in the next sueeessional stage. Howard and Ashton (1967) studied the viable seed stored under burnt and unburnt *Eucalyptus pauciflora* subalpine woodland at Lake Mountain, Vietoria, and eame to the conelusion that sueh seed may be as important as the eurrent seed crop in determining the eomposition of regenerating vegetation after fire.

In this investigation, the species eomposition of the buried viable seed in three vegetation types at West Downs (Surrey Hills, North West Tasmania) was determined, and the results related to the mosaie of communities observed in the area. Fires have played an important part in producing this mosaie, and it was hoped that buried viable seed eould provide further evidenee for the successional status of some vegetation types.

## GENERAL ENVIRONMENT

West Downs is located in the Surrey Hills, approximately 20 miles (32 km) south of Burnie, Tasmania. The area under study has a general elevation of 1900 ft (579 m), and is on the western boundary of an extensive Tertiary basalt plateau, which drops away sharply to the Hellyer River. Soils in the area are predominantly kraznozems (Stephens, 1962). The rainfall of the area is reliable and probably exeeeds 70 in (177 cm) p.a. Snow may oeeur in winter, but rarely persists for more than a week. The summers are mild, and the winters very eool, frosts may oeeur throughout the year, and in winter minima of –10°C are not uneommon.

The area under study (Fig. 1) eonsists of a small, shortly turfed grass plain surrounded on the north by mature *Nothofagus cunninghamii* elosed forest (Specht, 1970), on the east by mature and on the west by young mixed tall open euealypt forest/elosed *Nothofagus* forest. The boundary between the grassland and elosed *Nothofagus* forest is extremely abrupt, whereas the boundary between the western edge of the grassland and the young tall open forest/elosed forest is extensive, and a number of different phases ean be reeognized. Within one of these phases (dominated by *Acacia melanoxylon*) sampling for soil seed estimates was earried out.

## STAND DESCRIPTIONS

(1) *Closed Nothofagus cunninghamii forest.*

This stand (Fig. 1, V) consists of uneven aged

* Associated Forest Holdings Pty. Ltd., Burnie, Tasmania. Present address: School of Botany, University of New South Wales, Kensington, N.S.W. 2033.

*Nothofagus cunninghamii* and *Atherosperma moschatum* trees up to 120 ft (36·5 m) in height, with a combined crown cover of more than 75%. The understorey is sparse (less than 10% cover) but can be divided into a tall shrub (15-20 ft, 4·5-6 m) layer, mainly of *Drimys lanceolata* with occasional *Cenarrhenes nitida* bushes, and a diffuse tree fern stratum (8 ft, 2·4 m) dominated by *Dicksonia antarctica*. Ground cover by ferns (especially *Polystichum proliferum*) is very patchy. Grasses and herbs are absent, but mosses, lichens and liverworts are abundant on tree trunks, large branches and fallen logs, but only locally abundant on the soil. A litter layer of 1-2 in (2·5-5·0 cms) is well developed over the remainder of the forest floor, and may be up to one foot deep around the boles of old *Nothofagus* trees.

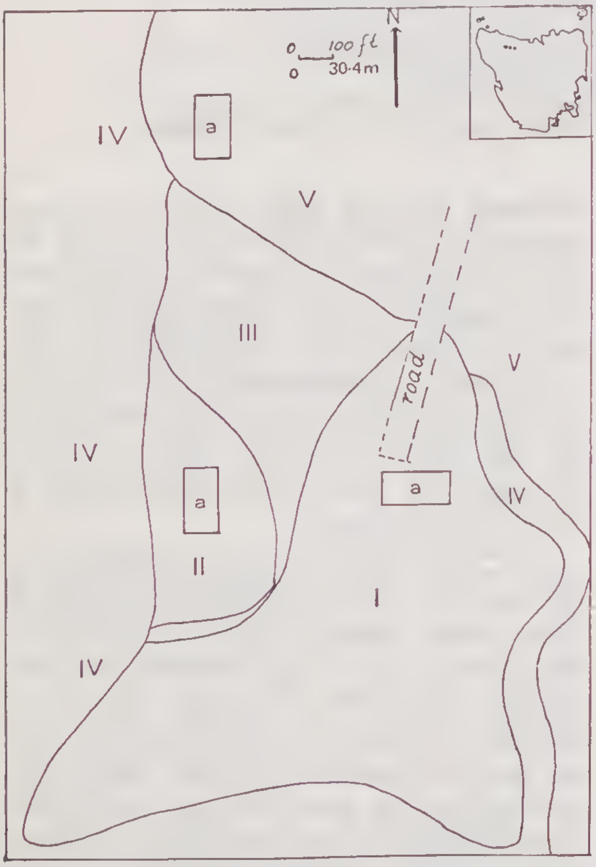


FIG. 1—West Downs plain and surrounding vegetation, to show sample sites. The inset of Tasmania shows the location of the Surrey Hills. I. *Poa gunnii – Hakea microcarpa*. II. *Drimys lanceolata – Acacia melanoxylon*. III. *Poa gunnii – Drimys lanceolata – Pteridium esculentum*. IV. *Eucalyptus delegatensis – Atherosperma moschatum – Nothofagus cunninghamii*. V. *Nothofagus cunninghamii – Atherosperma moschatum*. □ Areas within which soil-seed samples were collected.

This stand has probably been stable as closed *Nothofagus* forest for the last 400 years at least, and may have been undisturbed by external influences for 800 years or more (Howard, 1973a).

(2) *Grassland*

The grassland (Fig. 1, I) is dominated by *Poa gunnii* with *Agropyron pectinatum* locally abundant. Grass cover is continuous except for occasional hollows, which are waterfilled in winter, where a thin cover of *Polystichum* spp. is present. In the short springy turf numerous herb species occur, the most abundant being *Viola hederacea*, *V. betonicifolia*, *Gnaphalium collinum*, *Oxalis corniculata*, *Hydrocotyle sibthorpioides*, *Diurus pedunculata* and *Luzula campestris*. The moss *Thuidium furfurosum* var. *sparsum* is present throughout the turf, while the surface of the turf is dusted with individuals of *Cladia retipora*. Three shrub species are abundant throughout the grassland, *Lissanthe montana* (1 ft, 0·3 m), *Hakea microcarpa* which forms local thickets up to 10 ft (3·4 m) and *Drimys lanceolata* as individual shrubs up to 25 ft (7·6 m) tall.

It is probable that some at least of this grassy plain has been stable for a long time, as there is no evidence of tree charcoal and few irregularities in the plain surface which can be related to those within the closed *Nothofagus* forest. The presence of very narrow charcoal bands in the soil suggest that the plain has been maintained by fire, and the existence of a complex ecotone on the west shows that the plain may fluctuate in size.

(3) *The Ecotone*

Passing from the grassland to the tall open eucalypt/closed forest, various zones in the ecotone may be charactertized as:

(a) *Poa gunnii* and *Pteridium esculentum* equally abundant (included in III in Fig. 1).

(b) *Pteridium esculentum* dominant, *Poa gunnii* almost absent, *Drimys lanceolata* tall (15-25 ft, 4·5-7·6 m) shrubs very abundant (included in III in Fig. 1).

(c) *Pteridium esculentum* almost entirely replaced by *Histiopteris incisa*, ground cover absent in many places; *Drimys lanceolata* present as tall straggling shrubs (20-30 ft, 6-9 m) irregularly distributed under a tree stratum (70-80 ft, 21·3-24·3 m) of *Acacia melanoxylon*; ground-ferns and tree ferns abundant (II in Fig. 1).

Sampling was carried out in the last described zone. *Acacia melanoxylon* occurs as very large mature trees, carrying a rich flora of epiphytic mosses and lichens, a few liverworts and abundant

*Microsorium diversifolium* on main branches and trunks. Lichens and mosses (especially *Dicranoloma menziesii*) are abundant on the forest floor, over an aromatic litter layer 1-2 in (25-50 mm) deep. The total crown cover is high (more than 85%), so that this forest is even darker than the closed *Nothofagus* forest.

## METHODS

Soil was carefully excavated from five random sites, each measuring 12 x 12 in (300 x 300 mm) in each stand in August 1970. One inch deep slices of soil were collected for each replicate at 0-1 in, 1-2 in, 3-4 in and 5-6 in (25 mm, 25-50 mm, 75-100 mm, 125-150 mm). All samples were sieved in a laboratory to remove roots, corms, tubers, rhizomes and rock and were spread evenly in 12 x 12 x 2 in (300 x 300 x 50 mm) plastic trays. For both closed *Nothofagus* and *Acacia melanoxylon* forest, soils from 0-1 in (25 mm) and 1-2 in (25-50 mm) were shallow in the trays due to the high proportion of roots in these samples. This was particularly marked for the *A. melanoxylon* soil where more than half these samples was a mat of tree roots. The trays were placed in a glasshouse, and kept uniformly moist. All seedlings were identified, counted and removed as they appeared. After about four months the main flush of germination had passed, and the soil was turned over. As very little further germination occurred after one year, the majority of replicates was discarded at this time.

At the time of soil collection, all species present in the vicinity (c. 100 ft, 30 m) of the sample sites were recorded, and their cover class estimated.

## RESULTS

In Tables 1-3 the species germinating from each vegetation type and depth are shown in comparison with the angiosperm species present as living plants. After five to six months in the glasshouse both the *Nothofagus* and *A. melanoxylon* forest soils developed a dense cover of *Histiopteris incisa* and *Hypolepis australis*. Both these ferns occur in the present *A. melanoxylon* stand, but are absent from the *Nothofagus* forest. No tree fern or *Polystichum proliferum* plants developed. Some mosses developed on all soil samples but these were most abundant on the grassland soil, where *Polytrichum* sp. was very abundant. A few ferns developed from the grass-

TABLE 1

SPECIES COMPOSITION (ANGIOSPERMS) OF THE CLOSED *Nothofagus cunninghamii* FOREST COMPARED WITH THE SPECIES GERMINATING FROM THE SOIL AT EACH SAMPLE DEPTH. SPECIES NAMES FOLLOW CURTIS (1956-1967) AND WILLIS (1962).

| Species | Stand* | Density of germinable seed per square foot 0-1″, 25 mm | 1-2″, 25-50 mm | 3-4″, 75-100 mm | 5-6″, 125-150 mm |
|---|---|---|---|---|---|
| *Drimys lanceolata* | 2 | 4·6 | 2·4 | 0·6 | 0·8 |
| *Acacia melanoxylon* | | | 0·2 | | |
| *Coprosma quadrifida* | 1 | | | | |
| *Gaultheria hispida* | | | | 0·2 | |
| *Pittosporum bicolor* | † | | 0·2 | | |
| *Cenarrhenes nitida* | † | | | | |
| *Phyllocladus aspleniifolius* | † | | | | |
| *Atherosperma moschatum* | 3 | | | | |
| *Nothofagus cunninghamii* | 5 | | 0·2 | | |
| *Zieria arborescens* | | | 0·2 | 0·2 | |
| *Libertia pulchella* | 1 | | | | |
| *Luzula campestris* | † | 1·2 | 3·0 | 3·0 | 1·2 |
| *Agropyron pectinatum* | | 0·2 | | | |
| *Juncus* sp. | | 0·6 | 0·8 | 0·2 | 1·0 |
| *Poa gunnii* | | 0·6 | 1·6 | 2·6 | 0·4 |
| *Carex* sp. | | | 0·6 | | |
| *Hydrocotyle sibthorpioides* | | | 0·4 | 0·8 | 0·6 |
| *Acaena anserinifolia* | | 0·4 | 1·4 | | |
| *Viola hederacea* | | | 0·6 | 0·2 | |
| *Gnaphalium collinum* | | 0·2 | | | |
| *Hypericum japonicum* | | 0·2 | 1·4 | 1·6 | 1·8 |
| *Cotula filicula* | | | | 0·2 | |
| Total | | 8·4 | 12·6 | 9·6 | 6·0 |
| % Woody Species | | 59·5 | 22·2 | 42·0 | 13·3 |

* *Cover rating for species in existing stands*—†, *less 1%, 1, 1-5%, 2, 5-25%, 3, 25-50%, 4, 50-75%, 5, 75-100%.*

land 0-25 mm samples only. *Marchantia* sp. thalli appeared on the *Nothofagus* and *A. melanoxylon* soils.

The main points illustrated by Tables 1-3 are:
(a) The number of germinable seeds stored in the soil generally diminishes with sample depth.
(b) The smallest number of seeds was stored in the *Nothofagus cunninghamii* closed forest soil.
(c) None of the woody species present in the grassland germinated from grassland soils.
(d) Grasses, rushes, sedges and herbs, though largely absent from both *Nothofagus* and *Acacia melanoxylon* stands were well represented as seeds in these forest soils.

Of particular interest is the presence of *Acacia melanoxylon* seed in the *Nothofagus* forest soil although trees of this species are absent from the stand.

The majority of species germinated in the first six months after the soil was placed in the glass-house, although the majority of *Drimys lanceolata* seedlings did not appear until the following spring.

## DISCUSSION

The closed *Nothofagus* forest germination, 21 seedlings per 12 x 12 x 2 in (300 x 300 x 50 mm) is low when compared with the figure for a similar forest at Cement Creek, Victoria (120 seedlings per 12 x 12 x 2 in (300 x 300 x 50 mm) Carrol & Ashton, 1965). This may be a reflection of both the less diverse flora of the West Downs stand and of the greater age of the forest. The presence of herb, rush, grass and sedge species in the *Nothofagus* forest soil either reflects the longevity of some of these seeds (rush and sedge), or the ease with which they can be introduced from surrounding vegetation types (grass and herb).

The germinable seed present in the top two inches of the grassland soil (173) also appears to be low when compared with other grassy areas (e.g. red gum woodland, Yan Yean, 2303, Howard & Ashton, 1967). This may be due in part to the density of the sward (which was removed before soil collection) impeding seed penetration into the soil. Very heavy grazing of flowering grass heads by wallabies (*Macropus rufogriseus*) and wombats (*Vombatus ursinus*), may also be a contributing factor. Although woody perennials in general are often under represented by buried viable seed, the failure of any shrub species to germinate from this soil may be attributed to a different factor for each species. The fleshy fruits of *Lissanthe montana* are eaten as soon as they ripen, the hard follicles of *Hakea microcarpa* do not usually release viable seed

TABLE 2

SPECIES COMPOSITION (ANGIOSPERMS) OF THE CLOSED *Acacia melanoxylon* STAND COMPARED WITH THE SPECIES GERMINATING FROM THE SOIL AT EACH SAMPLE DEPTH.

| Species | Stand* | Density of germinable seed per square foot 0-1″, 25 mm | 1-2″, 25-50 mm | 3-4″, 75-100 mm | 5-6″, 125-150 mm |
|---|---|---|---|---|---|
| *Drimys lanceolata* | † | 6·4 | | | |
| *Acacia melanoxylon* | 5 | 1·4 | | 0·8 | |
| *Coprosma quadrifida* | † | 3·0 | | 0·4 | |
| *Gaultheria hispida* | | | 1·6 | | 0·2 |
| *Pittosporum bicolor* | † | 0·2 | | | |
| *Luzula campestris* | | 5·0 | 13·2 | 8·6 | 5·4 |
| *Agropyron pectinatum* | | 2·0 | 2·6 | 2·8 | |
| *Juncus* sp. | | 0·6 | 1·4 | 2·4 | 0·2 |
| *Poa gunnii* | | 0·6 | 0·4 | 2·4 | 0·4 |
| *Carex* sp. | | 4·4 | 8·8 | 15·6 | 6·4 |
| *Hydrocotyle sibthorpioides* | † | 46·4 | 48·8 | 35·8 | 16·2 |
| *Acaena anserinifolia* | † | 0·2 | 0·8 | | |
| *Geranium microphyllum* | † | 0·4 | 0·4 | | |
| *Oxalis corniculata* | † | 29·0 | 21·0 | 24·2 | 7·2 |
| *Australina pusilla* | † | 3·8 | 8·0 | 4·6 | 2·0 |
| *Cardamine intermedia* | † | 1·6 | 0·4 | 0·2 | |
| *Viola hederacea* | | 0·8 | 2·0 | 1·4 | 1·4 |
| *Gnaphalium collinum* | | 0·2 | 0·2 | | |
| *Hypericum japonicum* | | 1·2 | 1·2 | 4·0 | 1·6 |
| *Lagenophera stipitata* | | 0·2 | 0·6 | 0·6 | 0·2 |
| *Centaurium erythraea* | | | 0·4 | 0·4 | 0·2 |
| Total | | 107·4 | 111·8 | 103·2 | 41·4 |
| % Woody Species | | 10·2 | 1·4 | 1·2 | 1·4 |

**See Table 1.*

without the intervention of fire, and the seeds of *Drimys lanceolata* are extensively harvested by ants which live only in the grassland.

The seed stored in the soil of the *Acacia melanoxylon* forest (220 seeds per 12 x 12 x 2 in, 300 x 300 x 50 mm) is greater than for either grassland or *Nothofagus* forest. More than a third of this seed is of *Hydrocotyle sibthorpioides*, which is poorly represented in the vegetation at present.

The failure of most *Drimys lanceolata* seeds to germinate until a year after soil collection suggests that the abundant autumn 1970 crop had to undergo some 'pre-treatment' before it would germinate. Experiments with washing seeds, and the observation that seeds sometimes germinate on the shrubs after prolonged heavy rain suggests that there is a water soluble inhibitor involved in retarding seed germination.

The abundance of *Hydrocotyle sibthorpioides*, *Carex* sp., *Juncus* sp., and *Oxalis corniculata* in the *Acacia melanoxylon* forest soil support the supposition based on observation, that this stand is present as the result of burning. In the Surrey Hills district, when a *Nothofagus* or mixed *E. delegatensis*/*Nothofagus* forest is severely burnt, the early stages of succession are usually marked by an abundance of rushes, sedges, *Hydrocotyle sibthorpioides*, *Oxalis corniculata* and *Marchantia* sp. on the ground, regardless of which species of trees and/or shrubs have established. This early phase is usually followed after 1-2 years by rushes, sedges and fern species (*Hypolepis australis*, *Histiopteris incisa*) dominating the understorey. Should the tree or shrub stratum become sufficiently dense, all these species are suppressed and die. It appears, however, that these seeds and spores are stored for remarkably long periods in the soil. The *A. melanoxylon* stand in question has been present for at least 60 years, and the neighbouring *Nothofagus* forest, where *Carex* sp. and *Juncus* sp. still persist as seeds, is more than 400 years old. The presence of abundant *Carex* sp. seed in the grassland soil suggests that the grassland may also go through a phase, after fire, when this species is abundant before grass tussocks re-establish themselves.

*Nothofagus cunninghamii*, the dominant tree of the closed forest, was poorly represented amongst germinating seedlings from this forest soil. This is a reflection of the sampling time (August), as by this time of the year nearly all

TABLE 3

SPECIES COMPOSITION (ANGIOSPERMS) OF THE GRASSLAND, COMPARED WITH THE SPECIES GERMINATING FROM THE SOIL AT EACH SAMPLE DEPTH.

| Species | Stand* | Density of germinable seed per square foot 0-1", 25 mm | 1-2", 25-50 mm | 3-4", 75-100 mm | 5-6", 125-150 mm |
|---|---|---|---|---|---|
| *Hakea microcarpa* | 2 | | | | |
| *Lissanthe montana* | 1 | | | | |
| *Drimys lanceolata* | † | | | | |
| *Luzula campestris* | † | 17·0 | 8·8 | 4·2 | 2·4 |
| *Agropyron pectinatum* | 1 | 10·0 | 10·4 | 1·6 | 0·8 |
| *Juncus* sp. | | 0·6 | 0·4 | 0·4 | 0·2 |
| *Poa gunnii* | 5 | 5·2 | 2·4 | 1·6 | 0·6 |
| *Carex* sp. | | 17·2 | 14·6 | 4·4 | 2·4 |
| *Prasophyllum suttonii* | † | | | | |
| *Diurus peduncularis* | † | 40·2 | 4·8 | 0·8 | 0·2 |
| *Hydrocotyle sibthorpioides* | † | 0·4 | 0·4 | 0·6 | 0·2 |
| *Oxalis corniculata* | † | 0·2 | | | 0·2 |
| *Viola hederacea* | † | 2·2 | 3·4 | 1·0 | 0·6 |
| *Gnaphalium collinum* | † | 0·2 | | | |
| *Hypericum japonicum* | † | 20·4 | 12·2 | 6·4 | 0·8 |
| *Lagenophera stipitata* | | | | | 0·2 |
| *Centaurium erythraea* | † | 1·6 | 2·2 | 0·4 | |
| *Cotula filicula* | † | | | | |
| *Viola betonicifolia* | † | | | | |
| *Helichrysum scorpioides* | † | | | | |
| *Craspedia glauca* var. *gracilis* | † | | | | |
| *Leptorhynchos squamatus* | † | | | | |
| *Brachycome diversifolia* | † | | | | |
| *Oxalis lactea* | † | | | | |
| Total | | 115·2 | 59·6 | 21·4 | 8·6 |
| % Woody Species | | 0 | 0 | 0 | 0 |

**See Table 1.*

seed has decayed or been destroyed (Howard, 1973b), and more will not fall until the following February. The *Acacia melanoxylon* seed which germinated from the 1-2 in layer of this soil has probably been stored for an extremely long period, as no *A. melanoxylon* trees are present in the stand now.

The seeds of both *Nothofagus cunninghamii* and *Acacia melanoxylon* are relatively bulky (5 x 3 mm), but *Acacia melanoxylon* seeds are much less likely to be transported by wind and inseets, as they are 10 times heavier than those of *Nothofagus cunninghamii* (500/gm cf. 52/gm). This reinforces the supposition that the *Acacia melanoxylon* seed present in the mature *Nothofagus cunninghamii* stand has been stored in this soil, rather than transported to it.

The absenee of *Atherosperma moschatum*, the sub-dominant species in this forest, may also be due to the sampling time. but for this species seed set is irregular, whereas for *Nothofagus cunninghamii* it is regular and abundant. It is possible to conclude that a severe fire through this forest at most times of the year would result in a tall shrub dominated regeneration stand (*Drimys lanceolata*) with occasional *A. melanoxylon* as emergent trees. Only during the time of *Nothofagus* seed fall is there much chanec that a fire would be followed by the regeneration of a *Nothofagus* closed forest.

*Acacia melanoxylon*, which now dominates an ecotonal area between grassland and *Eucalyptus delegatensis/Nothofagus* forest has apparently been stabilized in this position by repeated fires which have prevented the re-establishment of eucalypts in the area. In other areas of West Downs the grassland abuts directly onto mixed *E. delegatensis/Nothofagus* forest without passing through a belt of *Acacia melanoxylon*. The re-establishment of an *E. delegatensis* dominated stand after one has been burnt, presupposes the existence of seed, either stored in the soil (poor supply usually), or in mature capsules in the tree crowns. Over most of Surrey Hills, *E. delegatensis* seed set is very irregular (up to four years may pass with no seed set (D. de Boer, pers. comm.)), and seed erops are often very light. It is not unreasonable to suppose, therefore, that the *A. melanoxylon* stand resulted originally from a fire (probably originating in the grassland) during a year in which no *E. delegatensis* seed was available, and that this fire burnt a short way into the mixed *E. delegatensis/Nothofagus* forest.

Although the mixed *E. delegatensis/Nothofagus* forest abutting the *Acacia melanoxylon/Drimys lanceolata* zone contains *Nothofagus* trees which flower regularly, no seedlings of *Nothofagus* were found in the *Acacia melanoxylon* stand, though they were abundant in the mixed forest. The very heavy shade cast by the *Acacia melanoxylon* trees presumably prevents *Nothofagus* regeneration, so that this forest type may represent an alternative climax form. It is quite probable that as *Acacia melanoxylon* trees die, they will be replaced by *Nothofagus* seedlings, thus the formation of a closed *A. melanoxylon* canopy may be only a temporary check in the succession to closed *Nothofagus* forest.

From these observations of the present vegetation, and viable soil stored seed, it has been possible to make some deductions about the past history of the vegetation and its possible future should a catastrophe such as fire occur. When such predictions are combined with observations of suspected seral stages in the Surrey Hills distriet, these stages become easier to interpret. Thus it would appear that, in an area such as Surrey Hills, of reasonably uniform soil, climate and topography, a considerable amount of evidenee can be gained from investigations of soil seed to support general hypotheses on the possible seral relationships between observed vegetation types.

## ACKNOWLEDGMENTS

The author wishes to thank Associated Forest Holdings Pty. Ltd., for their financial support, and Mr. D. de Boer for his help and encouragement throughout the project.

## REFERENCES

CARROL, E. J., & ASHTON, D. H., 1965. Seed storage in soils of several Victorian plant communities. *Vict. Nat.* 82: 102-112.

CURTIS, W. M., 1956-1967. *The Student's Flora of Tasmania*. Parts 1, 2, 3. Govt. Printer, Tasmania.

HOWARD, T. M. & ASHTON, D. H., 1967. Studies of soil seed in snow gum woodland (*E. pauciflora* Sieb. ex Spreng var. *alpina* (Benth.) Ewart). *Vict. Nat.* 84: 331-35.

HOWARD, T. M., 1973a. Studies in the ecology of *Nothofagus cunninghamii* Oerst. 1. Natural regeneration on the Mt. Donna Buang Massif, Victoria. *Aust. J. Bot.* 21: 67-78.

————, 1973b. Studies in the ecology of *Nothofagus cunninghamii* Oerst. 2. Phenology. *Ibid.* 21: 79-92.

OOSTING, H. J. & HUMPHREYS, M. E., 1940. Buried viable seeds in a successional series of old field and forest soils. *Bull. Torrey Bot. Club* 67: 253-73.

SPECHT, R. L., 1970. 'Vegetation' in "*The Australian Environment*". Ed. G. W. Leeper, 4th edition, CSIRO and Melb. Univ. Press.

STEPHENS, C. G., 1962. *A Manual of Australian Soils*. 3rd edit. CSIRO Melbourne.

WILLIS, J. H., 1962. *A Handbook to Plants in Victoria*. Vol. 1. Melb. Univ. Press.